Vol. 47 No. 1

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1920

Observations on monosporangial discs in the genus Liagora

MARSHALL A. HOWE

(WITH PLATE I AND FIVE TEXT-FIGURES)

The genus *Liagora* is a group of marine red algae of the family Nemalionaceae (Helminthocladiaceae). The species are confined to the warmer seas, where they show a preference for water that is normally agitated, ranging, however, from between the tide-lines on surf-beaten rocks down to a depth of at least one hundred feet. In the West Indian region, including Bermuda and southern Florida, the genus is represented by nine or ten species and one species is known to occur on the Californian coast. With the exception of one species, recently described from Bermuda by Collins & Hervey,* and one from the Mediterranean Sea, the plant body is more or less calcified, the amount of the lime and the way in which it is deposited being more or less characteristic of the various species. Under the compound microscope the thallus is seen to be of an obviously filamentous structure, both the structure and the often lubricous character of the plants when living sometimes calling to mind their fresh-water relatives of the genus *Batrachospermum*.

Most of the species of *Liagora* are consistently dioicous, others are consistently monoicous—characters that hitherto have been rarely ascertained or mentioned in the describing of species, probably because the antheridia are in some species very inconspicuous. The plants rarely seem to be sterile. Antheridia,

* Proc. Am. Acad. **53**: 100. 1917.

[The BULLETIN for December (**46**: 461–502. *pl. 19*) was issued December 31, 1919.]

procarps, or the subsequent cystocarps may nearly always be found, but the writer in examining some hundreds of specimens, has never seen anything that could be certainly interpreted as tetrasporangia or as a non-sexual alternating generation. In the older systematic works, it is either expressly stated that tetraspores in the genus *Liagora* are unknown or else silence is maintained on this point. In Schmitz's treatment of the genus in Engler & Prantl, Die natürlichen Pflanzenfamilien, we find, "Sporangien ungenügend bekannt, angeblich an knotig verdickten Stellen der oberen Thalluszweige aus den Endzellen der Rindfäden entwickelt und unregelmässig paarig geteilt." De-Toni, in his Sylloge Algarum, appears to have carried this statement over into Latin, omitting, however, to translate the "angeblich." Whether this statement by Schmitz rests upon his own personal observations or is based upon some previously published observation that has escaped the attention of the present writer is not clear. Oltmanns, in his Morphologie und Biologie der Algen, is apparently silent in regard to this matter.

In Kützing's Tabulae Phycologicae (**8**: 43. *pl. 90 I.* 1858) we find in his delineations of *Liagora Turneri* from the Red Sea a figure showing "Ein Gliederfaden, dessen eine Zelle sich zu einer Brutzelle erweitert, aus welcher sich die in *d. e. f. g. h. i.* dargestellten Knospen entwickeln, welche der Anfang der Seitensprossen sind." Structures evidently similar to those figured by Kützing occur in at least four of the West Indian species of *Liagora* (*L. ceranoides*, *L. valida*, *L. farinosa*, and *L. pinnata*), which often show small flat orbicular discs lying on the general surface of the plant or somewhat immersed among the assimilatory filaments. These discs are of a deeper red color than the main *Liagora* plant, they send down few or numerous roothairs from their ventral (proximal) surface in among the assimilatory filaments, and they bear on their dorsal (distal) surface a few sporangia, the contents of which remain undivided, so that they may referred to as monosporangia. Long, colorless, gelatinizing hairs may usually be seen, arising from this outer or dorsal surface. The disc is involved in mucus, the outer limits of which may be distinct or may be vague or imperceptible. Except in the youngest parts of the *Liagora*, this mucous envelope is more or less calcified. These

monosporangium-bearing discs look at first sight very much like independent epi-endophytes. Their darker red color, their dorso-ventral rather than radial symmetry, and the lack of any obvious genetic continuity with the *Liagora* give plausibility to the very natural first impression that they are independent organisms or perhaps obligate epiphytes of various species of the genus *Liagora*. Another plausible *a priori* hypothesis would be that they result from the germination of carpospores and represent a non-sexual alternating phase in the life-history of the *Liagora*. But in support of this latter hypothesis, the present writer finds no direct evidence at all, and the fact that in *L. farinosa* these monosporangial discs are commonly more abundant on antheridial than on cystocarpic plants would seem to point to its improbability. The truth seems to be that these discs arise from gonidia, gemmae, or aplanospores, derived from the terminal or subterminal cells of the assimilatory filaments of the *Liagora*, as was the view of Kützing in regard to similar structures in *Liagora Turneri*. Kützing appears to be the only one who has previously alluded to these structures in print and his observations appear to have been overlooked or ignored by subsequent writers on the genus. These monosporangial discs are especially common in West Indian specimens of *Liagora ceranoides* Lamour. (*L. pulverulenta* Ag.) and *L. farinosa* Lamour. (*L. elongata* Zan.), occurring on both antheridial and cystocarpic plants. In *L. ceranoides*, the gemmae are unicellular or bicellular, terminal or subterminal, solitary or concatenate, but are most frequently derived from the terminal (distal) cells of the assimilatory filaments. The cell enlarges, its contents become deeper red, its walls become soft and mucous, and a new cell wall is laid down inside the old one (FIGS. 1 and 2). Sometimes the rejuvenated cell or aplanospore escapes from the old wall before germinating, but nearly always in this species, as in *L. valida* Harv., germination takes place, or at least begins, *in situ*. The original wall, however, becomes so tenuous that the aplanospore or young disc is very easily detached from its place of origin and even when it develops in its original position, the original walls dissolve so completely that it is usually very difficult to assure one's self of its genetic connection with the filament from which it was derived. Occasionally, the cell, with its original

wall is abjointed as a one-celled gemma, but when abjointing occurs the subjacent cell commonly goes with it, the two together (FIGS. 7 and 8) constituting a two-celled gemma. In this case, the lower of the two cells seems not to divide but to persist as a finally inconspicuous stalk or appendage of the young disc, which results from divisions of the upper cell (FIG. 22). Very rarely (FIG. 28), one finds an irregular pluricellular gemma formed without obvious rejuvenescence or with rejuvenescence limited to one or two of its cells. Occasionally (FIG. 9) several consecutive

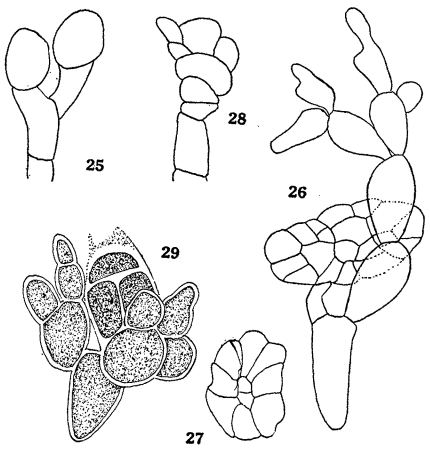


FIG. 25. Terminal cells of an assimilatory filament of *Liagora ceranoides* (No *4778d*, from Montego Bay, Jamaica), showing enlargement and rounding of two of them preparatory to their division to form multicellular gemmae, which develop into monosporangium-bearing discs. × 510.

FIG. 26. A later stage, showing young disc, still attached, disc and stalk-cell together corresponding to a twice forked vegetative branch four cells long (No. *4778d*), × 620.

FIG. 27. Dorsal view of a young disc, slightly smaller than that shown in FIG. 26 (No. *4778d*). × 260.

FIG. 28. Apex of an assimilarity filament showing irregular division to form a gemma (No. *3141*, *L. ceranoides*, Gun Cay, Bahama Islands). × 620.

FIG. 29. A gemma in a three-celled stage, the original mother-cell wall gelatinizing at apex (No. *3141*). × 510.

cells of a filament are converted into aplanospores with evident rejuvenescence and with gelatinization of the original walls. The first divisions of the rejuvenated cell appear to occur in a variety of ways. Often (FIGS. 8 and 29) they suggest the "cru-

ciate" or tripartite divisions of a tetrasporangium and structures of this character may have been responsible for the current somewhat vague and uncertain allusions to the existence of tetraspores in the genus *Liagora*. Occasionally the arrangement of the first segments of the young disc suggests that of the carpels of an orange, sometimes in apparent contravention of the usual rule that a cell divides in a plane perpendicular to its longest axis. When the young disc develops to a manifestly flattened form while still in its original orientation to the parent filament, it is seen (FIGS. 3, 4, and 6) that one of its edges is directed towards the filament, while the first root-hairs (FIGS. 5 and 22), ventral and central as regards the disc, are lateral in respect to the filament.

In *Liagora farinosa* Lamour. and *L. pinnata* Harv., the genetic connection of these discs with the *Liagora* is even more difficult to trace than in *L. ceranoides* and *L. valida*, owing, apparently, to the fact that the aplanospores are released from the more rigid mother-cell walls before germination, so that they do not germinate *in situ*. Hyaline, apparently unicellular hairs, usually several times as long as the diameter of the disc, arise from the dorsal surface and are probably always normally present in younger conditions at least, but owing to their delicacy and to their apparent readiness to dissolve into mucus, they are not always visible, especially in *L. ceranoides*, and they are not represented in our figures (FIGS. 6 and 18) of the disc in this species. The mature discs are suborbicular and are more or less similar in the four species of *Liagora* in which they have thus far been observed by the present writer, yet they show differences corresponding to the peculiarities of the species of which they constitute a part. In *L. ceranoides* and *L. valida*, the discs are softer, more mucous, and less compact than in *L. farinosa* and *L. pinnata*, in which the cells of the disc, like those of the assimilatory filaments of the main plant, have firmer, more rigid walls. In *L. valida*, the discs are thickened in the central part and often radiately unistratose towards the margins, while in *L. ceranoides* the discs give the impression of consisting of more than one layer of cells throughout. Fertile discs are mostly 90–230 μ broad (not including the mucous envelope), though in *L. farinosa*, the plants of which are commonly

the largest of the four species named, they may occasionally reach a diameter of nearly 400 μ. The monosporangia are ellipsoid, ovoid, or obovoid, and are usually 13–26 μ long and 13–18 μ broad, measuring protoplasts only. To what these monosporangia give rise on germination has not been determined but there seems to be some ground for believing that they produce monosporangial discs like those from which they sprang. Species of *Liagora* offer a favorable matrix for the germination of various filamentous algae, including species of *Acrochaetium*, *Ceramium*, and other Rhodophyceae, and inferences that young sporelings associated with a *Liagora* represent stages in development of the *Liagora* itself demand rigorous confirmation, such as might be supplied by cultures or by the presence of a complete series of developmental stages. In this connection, however, it may be remarked that the almost constant association of *Acrochaetium*-like forms with various species of *Liagora* is a suspicious circumstance that deserves further investigation.

In offering the above explanation of the origin of the peculiar monosporangium-bearing discs of certain species of *Liagora*, the writer realizes that he may be charged with having mistaken accidental contact for organic continuity. It would be easier, more conventional, and (*a priori*) more probable to regard the discs as independent or obligate epi-endophytes. Early in his acquaintance with them, the writer was at one time on the point of describing them as representing a new genus of uncertain family, but was deterred by observing that the character of the discs, particularly of their cells and cell walls varied according to the species on which they occurred, and that the discs were progressively older from base to apex of the *Liagora* thallus, the early stages being found only at the extreme apices. The chromatophores, too, seemed similar, except that those of the discs were more red than those of the vegetative cells of the *Liagora*, often as red as those of the carpospores. After much searching, indications that the discs could be traced back to certain cells of the *Liagora* thallus were observed, as shown in the accompanying figures. These observed evidences of direct continuity were not so numerous as the writer might wish and he knows of no analogy among other Rhodophyceae for the state of things here

alleged to occur in *Liagora*. However, he believes the above explanation of the origin of the discs to be correct and ventures to publish his observations in the hope that some one more favorably situated, perhaps with access to living material, with facilities for cultural experiments, and with a taste for cytological investigations, may be able to confirm or disprove them. The possibility that the discs represent an obligate epi-endophyte with a boring parasitic spore deserves special consideration.

THE NEW YORK BOTANICAL GARDEN

Explanation of plate 1

The material from which the drawings on this plate were made was obtained from four species of *Liagora*, all collected by the writer at Montego Bay, Jamaica.

1. Terminal cells of an assimilatory filament of *Liagora ceranoides* (No. *4778d*), showing enlargement and rounding of two cells preparatory to their division to form discs. × 620. (The relations of the branches have been somewhat disturbed and distorted by manipulation)

2. Enlarged terminal cell of an assimilatory filament of *L. ceranoides* (No. *5034*), showing gelatinization of apical portion of wall of original cell and formation of new wall for the rejuvenated cell. × 620.

3. A young few-celled disc of *L. valida* (No. *4778c*), still connected by mucus with the filament from the terminal cell of which it has apparently originated. × 375.

4. A young disc of similar size but with more numerous and smaller cells, the disc p obably representing a branch of the filament against which it lies (No. *4778c*—*L. valida*). × 375.

5. A young disc showing its first root-hair and connected by mucus with the filament from the terminal cell of which it was apparently derived (No. *4778c*—*L. valida*). × 375.

6. A young disc in *L. ceranoides* (No. *5034*), with a mucus connection with the end of the filament from the terminal cell of which it was apparently derived. × 375.

7. A two-celled gemma in *L. ceranoides* (No. *4778d*) about to be abjointed. × 620

8. A later stage in the development of a similar gemma after detachment, the distal cell now divided into three cells and the proximal cell remaining undivided, forming a sort of stalk to the young disc (*L. ceranoides*, No. *4778d*). × 620.

9. The terminal portion of an assimilatory filament of *L. ceranoides* (No. *4778d*), showing the formation of several unicellular gemmae or aplanespores in a more or less concatenate series. × 510.

10. A supposed free aplanospore or unicellular gemma before its first division (*L. ceranoides*, No. *4778d*). Possibly, however, a spore from a monosporangium of a matured disc. × 510.

11. A young five-celled disc in which all of the divisions appear to have been lengthwise of the mother-cell, with the first root-hair originating from near one of the poles (No. *4778d*). × 510.

12. A young four-celled disc in which the first division appears to have been lengthwise of the mother cell, followed by the transverse division of one of the daughter-cells (No. *4778d*). × 510.

13. A later stage in the development of a disc, but showing a shorter root-hair (No. *4778d*). × 620.

14. An older stage, with long root-hair and with suggestion of a short stalk at one edge, indicating origin of the disc from a two-celled gemma as shown in Figures 7 and 8 (No. *4778d*). × 272.

15. Dorsal view of a young disc, suggesting discs of species of *Erythrotrichia* and *Erythrocladia* but apparently belonging in the present series (*L. valida*, No. *4778c*). × 510.

16. A later saucer-shaped stage, seen more or less edgewise, and showing three hairs springing from the dorsal surface in its thicker central part and one root-hair from its ventral surface (*L. valida*, No. *4778c*). × 272.

17. Dorsal view of a nearly mature disc with two monosporangia. The dorsal hairs have deliquesced or are so very inconspicuous that no attempt has been made to represent them. The dotted outer line indicates boundaries of the peripheral mucus or gelatinized outer walls. (*L. valida*, No. *4778c*). × 350.

18. An obliquely dorsal view of a mature disc with several monosporangia (*L. ceranoides*, No. *4778d*—edges of disc less monostromatic than in *L. valida*). × 272.

19. Escape of aplanospore from terminal cell of assimilatory filament of *L. farinosa* (No. *4775*). × 375.

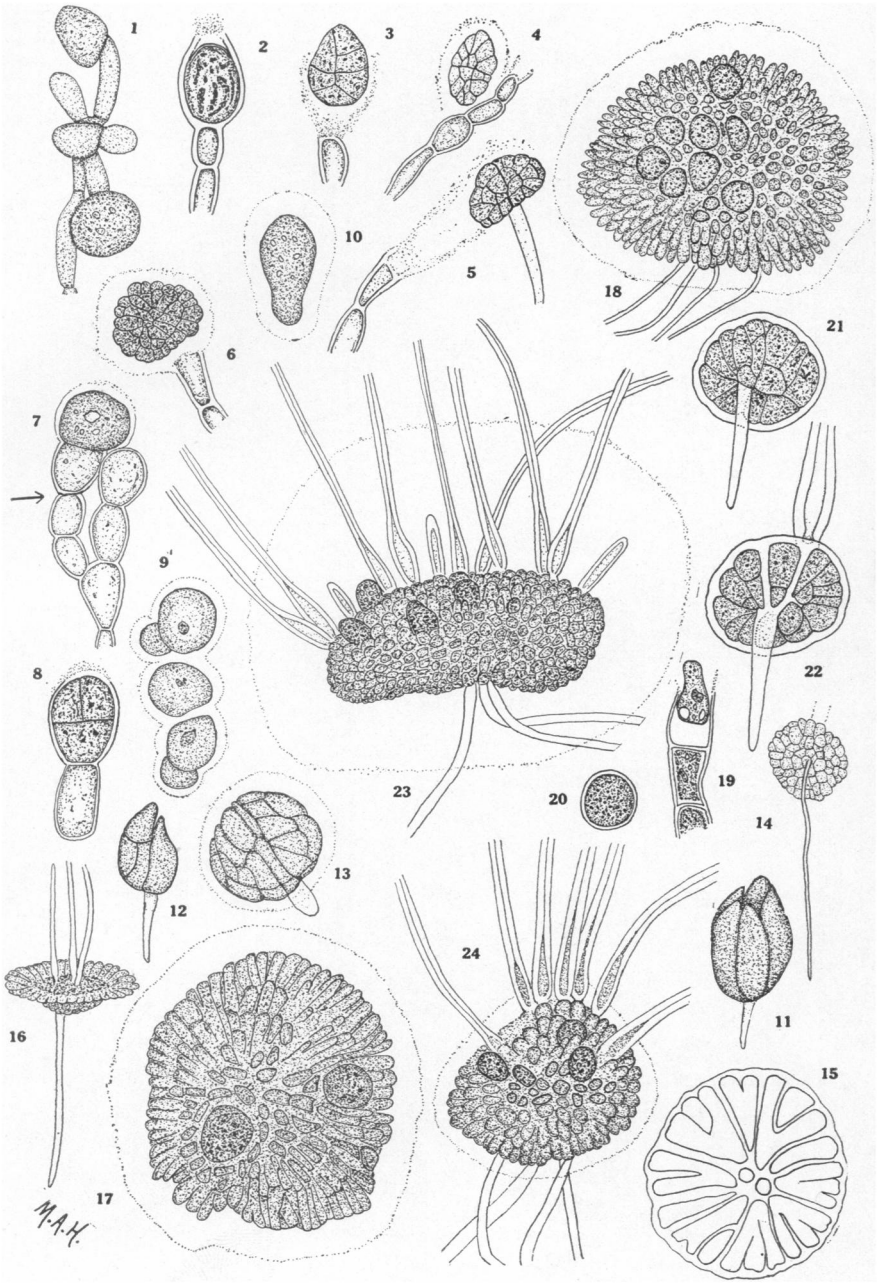
20. A free aplanospore from the same plant (No. *4775*). × 375.

21. A young disc of *L. farinosa* (No. *4775*) in ventral view, showing first root-hair. × 620.

22. Another young disc in obliquely ventral view (No. *4775*), showing base of first hair from dorsal surface and first root-hair. × 620.

23. A mature or nearly mature disc of *L. farinosa* (No. *4775*), in lateral view, showing the more or less protuberant monosporangia. The dotted line indicates the boundary of the mucus envelope, which, in the natural state, is lightly permeated with lime. Only about one third of the length of the dorsal hairs is shown. × 272.

24. Obliquely dorsal view of a mature or nearly mature disc of *L. pinnata* (No. *4776*), with monosporangia, etc. × 272.



HOWE: MONOSPORANGIAL DISCS IN LIAGORA